ResearchGate

See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/256091142

Patterns of size separation in carnivore communities

Chapter · January 1996

DOI: 10.7591/9781501745829-013

CITATIONS
70

READS
262

2 authors:

Tamar Dayan
Tel Aviv University
232 PUBLICATIONS **12,273** CITATIONS
SEE PROFILE

Daniel Simberloff
University of Tennessee at Knoxville
366 PUBLICATIONS **63,853** CITATIONS
SEE PROFILE

All content following this page was uploaded by Tamar Dayan on 29 September 2015.

The user has requested enhancement of the downloaded file.

CHAPTER 7

Patterns of Size Separation in Carnivore Communities

TAMAR DAYAN AND DANIEL SIMBERLOFF

Carnivores often range quite widely, and many species occur in a wide variety of biotic and abiotic environments. Different populations of the same species are often found under different climatic conditions, and may also coexist, in different communities, with different suites of potential prey and competitors. Thus, different carnivore populations may be subject to different selective pressures. These differences in selective regimes are probably reflected in differences in a variety of biological traits, the most conspicuous of which is body size. Many ecological and evolutionary studies have therefore dealt with morphological variation among carnivores.

Autecology: Ambient Temperature as a Selective Force

Many studies have treated the effect of climate on carnivore body size. Much research has demonstrated that body size in some carnivores is correlated with mean ambient temperature or latitude, the latter taken to be a surrogate for temperature (e.g., Davis 1981; Klein 1986). Temporal size change related to paleoclimatic change has also been demonstrated (e.g., Kurtén 1965; Davis 1977, 1981; Klein 1986). These phenomena accord with Bergmann's rule (Bergmann 1847), redefined by Mayr (1956, 1963), which states that the body size of homeotherms from cooler regions tends to exceed that of conspecific populations from warmer regions. Bergmann's explanation of this rule was that, because body volume (which produces heat) increases more rapidly than does corresponding body surface area (which dissipates heat), larger mammals produce more heat and lose less to the environment than do smaller ones. Large body size must then be adaptive for existence in cold climates.

Bergmann's rule is only one of several ecogeographic rules, empirical generalizations that define relationships between morphological variation and the physical environment, but it is the best studied of those rules and the only one

that has been intensively explored for carnivores. Thus the importance of the role of ambient temperature as an evolutionary force that affects the body size of mammals in general, and of carnivores in particular (see, for example, Klein 1986), is now widely accepted. A cursory review of the published literature, however, reveals that two-thirds of the carnivore species studied display some deviation from Bergmann's rule, at least in parts of their ranges (Dayan et al. 1991; see also Gittleman 1985). These deviations may derive, in part, from differences in the composition of the communities in which the different carnivore populations are embedded: coexistence with different potential competitors may have affected the sizes of these carnivores (Dayan et al. 1991).

Synecology: Competition as a Selective Force

Research on the possible evolutionary effect of interspecific competition on carnivore morphology has a venerable history. For many years numerous studies of various animal taxa have interpreted morphological size relationships among sympatric species of similar ecological requirements as indirect evidence for competition. Coexistence of competitors has been viewed as leading to coevolutionary change. Brown and Wilson (1956) defined character displacement as a phenomenon that may arise when two similar animal species overlap geographically: the differences between them may be accentuated in the zone of sympatry and weakened or lost entirely in parts of their ranges outside this zone. Character displacement might be generated by selection against hybridization or by selection to reduce competition for limiting resources. It is the latter possibility that concerns us. Hutchinson (1959) theorized that competition for food might impose a limit on the similarity between trophic apparati of potentially competing species. He saw different sizes as enabling different species to use different sizes of food. Starting with Holmes and Pitelka (1968), many researchers on groups of three or more species reported overdispersion of the mean sizes—a tendency toward equal size ratios between species adjacent in a size ranking (references in Simberloff and Boecklen 1981). Strong et al. (1979) termed this phenomenon "community-wide character displacement."

The positive relationship between body size and prey size among carnivores (Gittleman 1985) makes the hypothesis of food-size partitioning among them a reasonable one. Generally, larger predators take a larger range of prey sizes, primarily because of an increase in the upper size limit (Schoener 1969; Wilson 1975; Gittleman 1985). This evidence, coupled with a rich literature documenting aggressive interference among carnivores competing for prey (discussion and references in Van Valkenburgh 1984; Van Valkenburgh and Hertel 1993), enhances the suitability of carnivores for the study of character displacement. Therefore, among studies of character displacement in mammals,

carnivores have been the most prominent, even though they are difficult to study in the field.

Fuentes and Jaksic (1979) argued that character displacement occurs between two Chilean foxes (the colpeo fox, *Dusicyon culpaeus*, and the Argentine gray fox, *D. griseus*) that diverge in body length with increasing latitude, a phenomenon they attributed to increased habitat overlap. Jiménez (1993), however, failed to confirm this result, finding both fox species increasing in size with increasing latitude, in accord with Bergmann's rule. Rosenzweig (1968), McNab (1971), and Ralls and Harvey (1985) all studied the possibility of character displacement in North American weasels and arrived at conflicting conclusions. Rosenzweig (1968) attributed little of the geographical size variation of the stoat, or ermine (*Mustela erminea*), to competition with other weasels, or to size of potential prey, and saw key roles for mean annual temperature and latitude. He studied males and females separately and a mixed population of both. McNab (1971) interpreted the size variation within the same species as resulting from the combined effect of the size of the available prey and character displacement. In both studies the character measured was head plus body length. McNab (1971) arrived at similar conclusions for South American felids. In fact, he suggested that Bergmannian size clines, where found, were only a by-product of selection resulting from interspecific competitive interactions.

Ralls and Harvey (1985) used the condylobasal length of the skull as a measure of body size for the North American weasels and found no evidence of character displacement between any two species. They found that, for *M. erminea*, size increased with latitude and that there were no obvious correlates of size in the longtailed weasel (*M. frenata*) or the common or least weasel (*M. nivalis*). For the ermine, Ralls and Harvey (1985) also examined a number of other measures, including several they considered directly related to feeding, and found such high correlations between these and condylobasal skull length that they restricted their analyses to the latter. Because of the relatively high degree of sexual size dimorphism in weasels, McNab (1971) and Ralls and Harvey (1985) analyzed the two sexes separately and compared males to males and females to females when seeking character displacement.

Until recently, no comparably thorough analyses had been carried out on Old World weasels. Hutchinson (1959) and Williamson (1972), however, had pointed out that *M. erminea* in Ireland, where it occurs alone, is smaller than *M. erminea* in Britain, where *M. nivalis* is also present. Dayan and Tchernov (1988), further, suggested that the large size of *M. nivalis* in Egypt and on some Mediterranean islands results from character release (*sensu* Grant 1972) in the absence of larger congeners.

Kiltie (1984) studied size ratios among sympatric Neotropical cats using several measures—body weight, body length, relative maximum bite force, and relative maximum gape (estimated partly from jaw length). For each trait, ratios were computed between pairs of species adjacent in a size ranking. Thus,

for n species, there are $n - 1$ ratios. When all six species were analyzed, he found that none of the four sets of ratios was statistically distinguishable from those that would have been expected if the species sizes had been independently and randomly chosen between the smallest and largest observed sizes. Ratios for maximum gape among just the four largest species were significantly more similar to one another, and the minimum ratio was significantly greater than expected by chance, patterns he thought might have been generated by interspecific competition. He noted that the two smallest species, the margay (*Felis wiedii*) and the jaguarundi (*F. yagouraoundi*), were very similar in maximum gape, but that this similarity may have been permitted by different habitat use—where they are sympatric, the former species is more arboreal and the latter more terrestrial. Despite the sexual size dimorphism in these species, Kiltie (1984) studied a mixed sample of males and females, using averages or midpoints of ranges.

Later Kiltie (1988) extended his analysis of size relationships in Neotropical cats to field assemblages in tropical Africa and Asia. He suggested that jaw length correlates well with modal prey size. Using means of this character for sexually mixed samples, he found that all assemblages contained two species that are indistinguishable in jaw length. When those were treated as a single species he found assemblage-wide ratio regularity. The ratios were more similar to one another than would have been expected if the sizes were independent and random. Again, he viewed this pattern as conceivably generated by competition, and he noted that the two species that were very similar in size in each assemblage always differed in some other way: one was terrestrial and the other arboreal, or one used mesic and the other xeric habitats, or one had a dappled coat and the other a plain one.

The Controversy Surrounding the Role of Competition in Selecting for Size

Recently, much of the ecological literature on size relationships has been reconsidered and contested. Controversy surrounds the community-ecology literature that deals with morphological coevolution among competitors (e.g., Lewin 1983; Pimm and Gittleman 1990). This controversy casts doubt upon both the morphological/evolutionary role of competition and its role in structuring ecological communities.

Statistical Tests

Grant (1972, 1975) criticized some published cases of ecological character displacement and suggested that they could be otherwise interpreted. When studies claiming size-ratio equality and unusually large minimum size ratios

were subjected to rigorous statistical analysis, it appeared that, for a large fraction of claimed instances of size displacement, observed sizes did not falsify a hypothesis of independence between species (Roth 1981; Simberloff and Boecklen 1981). Schoener (1984) has questioned the power of these tests to detect deviation of a set of sizes from a random arrangement, and several authors (references in Simberloff 1989) questioned whether the main test used for ratio equality, the Barton-David test (Barton and David 1956; Simberloff and Boecklen 1981), is the most powerful available. There has been no full test of relative power, but the most extensive examination to date (Arita 1993) suggests that Barton-David tests are generally at least as powerful as others suggested and often more powerful. Arita (1993) finds, however, that no test is very powerful when there are very few sympatric species. Tonkyn and Cole (1986) pointed out that the Barton-David test estimates the largest and smallest possible sizes by those observed, and that this procedure introduces some error into the calculation of tail probabilities for observed deviation. This problem seems unavoidable and obtains for alternative tests as well (Simberloff 1989), but it should not lead to great errors unless species numbers are very small.

Guild Composition

Studies dealing with ecological character displacement and community-wide character displacement were criticized not only for lack of suitable statistical tests but also for choice of potential competitors (Simberloff and Boecklen 1981). Different choice of possible competitors as guild members may, of course, lead to conflicting results. Morphological studies dealt with members of a guild, a concept that has been interpreted in several ways (reviewed by Simberloff and Dayan 1991). Root (1967) defined ecological guilds as groups of species using the same class of resources in a similar way. The major discrepancy among various researchers' studies and interpretations has been the significance of the "similar way" in which resources were supposed to have been garnered. Although Root (1967) emphasized its significance, others have questioned it: "To state the question with a bit of hyperbole, does it matter that a particular insect species is captured by a silken spider web as opposed to a bird's beak? The ecosystem and community consequences are similar—one less insect of that species—and manner is irrelevant from the specific perspective" (Hawkins and MacMahon 1989:443).

Jaksic et al. (1981) and Jaksic and Delibes (1987) viewed the carnivores in their studies as part of a general predatory guild that also included owls, raptors, and snakes, clearly underplaying the role of "similar manner" in the way prey were sought and taken. Van Valkenburgh (1985) used a narrower definition of predatory guilds, including only extant and extinct mammalian predators. In her guild of large land predators, she included the nonaquatic,

nonvolant mammal species within a community that take prey and potentially compete for food. Van Valkenburgh (1985) limited guild membership to species above jackal size (7 kg), because she expected increased competition among large predators and also because these are better represented in the fossil record. None of these studies directly measured interactions among species within the designated guilds.

Other investigators (e.g., McNab 1971; Fuentes and Jaksic 1979) have simply studied congeneric species, assuming that closely related species are the most likely to compete with one another. One advantage of the guild concept stressed by Root (1967) is that it focuses attention on all sympatric species involved in a potentially competitive interaction, regardless of their taxonomic relationships. Guild designations, however, still tend to include closely related species, collectively termed "taxon-guilds" by Schoener (1986).

Another concern was that, although studies that were perceived to demonstrate character displacement and community-wide character displacement were readily published, it is more than likely that many others that *failed* to detect any morphological pattern were *not* reported, and accordingly there is a publication bias toward supportive evidence (Simberloff and Boecklen 1981). Even within the taxa of a given region there would be a tendency to emphasize the morphological patterns in certain guilds while neglecting those in others.

Choice of Characters

Another problem with studies of morphological relationships has been that different researchers choose different characters to measure (Simberloff and Boecklen 1981). Choice of different measures may, of course, yield different results. Hutchinson (1959) specified that minimum size ratios should occur between trophic apparati, but for mammals, surprisingly, he suggested skull length as a measure. Later studies used this measure or used measures of body size such as head plus body length. In recent years there has been a growing realization that trophic apparati more directly related to feeding should be studied. Thus Ralls and Harvey (1985) measured several "feeding" characters—length of the lower jaw, upper carnassial length, and others—for North American weasels, as did Kiltie (1984) for Neotropical cats. In his study of sexual size dimorphism in the genus *Mustela*, Holmes (1987), too, chose several characters related to feeding ecology. The characters chosen for these studies were generally related to the feeding behavior, but not primarily the killing behavior, of these carnivores.

In sum, there has been a frequent failure to justify the species viewed as guild associates, especially with respect to how prey are taken. Traits taken to represent size have also often been rather casually selected. Both of these problems cast doubt on the robustness of many conclusions. The use of statistical tests

has introduced an element of objectivity and rigor into the study of size separation, but more research is needed on the power of key tests.

Morphological Relationships among Israeli Carnivores

Israel supports a diverse carnivorous fauna of 16 extant terrestrial, nonaquatic species. This diversity stems from both geographical and historical factors (Yom-Tov and Tchernov 1988). Israel is situated at a biogeographic crossroads, a meeting point for fauna and flora from different biogeographic origins and of different biogeographic distribution (see, for example, Tchernov 1988). For many species Israel is at either the northernmost or the southernmost end of the range. Thus for several carnivore species, Israel and, perhaps, contiguous areas form a narrow zone of overlap, where carnivores that have not coevolved over most of their distributional ranges must coexist. If morphological coevolution among carnivores does occur, one should ask how these carnivores react to each other's presence in sympatry and whether ecological character displacement is seen in this zone. Our studies of Israeli carnivores (Dayan et al. 1989a, b, 1990, 1992a) differed from previous carnivore studies in several significant respects.

Composition of Israeli Guilds

We divided Israeli carnivores into guilds based on their limb morphology, which reflects and affects their locomotor behavior (cf. Van Valkenburgh 1985). The locomotor abilities of a carnivore reveal much about its way of life, preferred habitat, foraging behavior, and escape strategy (Van Valkenburgh 1984; see also Taylor 1989). We reasoned that carnivores that are similar in their locomotor behavior seek and take prey in a similar manner and are thus likely to encounter and to take similar spectra of prey species (Dayan et al. 1992b). We thus attached much significance to the way in which resources were taken, in the original spirit of Root's (1967) guild definition. Using these criteria we divided all of Israel's terrestrial nonaquatic carnivores into three guilds (Dayan et al. 1992b), excluding the striped hyena (*Hyaena hyaena*), a scavenger that feeds largely on carcasses and specializes in crushing bones (Ewer 1973). Hyenas have highly developed forelimbs and disproportionately small hindquarters, a specialized limb morphology that may be associated with the mechanics of bone crushing (Ewer 1973). Its ecology, morphology, and diet set the hyena apart from other Israeli carnivores.

Thus we studied morphological relationships among the other Israeli carnivores within their respective guilds. We found that morphological criteria provide a clearcut guild definition. The three guilds are:

1. Mustelids/viverrids—elongated, small to medium-sized, short-limbed pentadactyl plantigrades to semiplantigrades (Novikov 1962; Harrison 1968;

Osborn and Helmy 1980). There is no reduction of the ulna, and the radius retains the primitive ability to rotate around it. This guild comprises five species: four mustelids (the European badger, *Meles meles;* the ratel, or honey badger, *Mellivora capensis;* the beech marten, or stone marten, *Martes foina;* and the marbled polecat, *Vormela peregusna*) and one viverrid (the Egyptian mongoose, *Herpestes ichneumon*) (Dayan et al. 1989a).

2. Felids—carnivores having the feet digitigrade, with five toes on the forefeet but only four on the hindfeet (see, for example, Harrison 1968). The radius retains the ability to rotate around the ulna, thus enabling cats to grip with their forefeet, which is essential for climbing but also enables them to manipulate prey. No material was available for the now extirpated lion (*Panthera leo*) and cheetah (*Acinonyx jubatus*). Thus we studied only the small felids—the European wild cat (*Felis silvestris*), jungle cat (*F. chaus*), and caracal (*F. caracal*) (Dayan et al. 1990). The only large felid currently found in Israel, the leopard (*Panthera pardus*), is intermediate in size between the cheetah and the lion.

3. Canids—carnivores of open areas highly adapted for cursorial locomotion, the feet digitigrade, with five toes on the forefeet but only four on the hindfeet (Clutton-Brock et al. 1976). Canids are unable to rotate the foreleg, and accordingly cannot use them to manipulate prey (Taylor 1989). The gray wolf (*Canis lupus*), golden jackal (*C. aureus*), red fox (*Vulpes vulpes*), Ruppell's sand fox (*V. rueppelli*), and Blanford's fox (*V. cana*) are members of this guild in Israel (Dayan et al. 1992a). For the Middle Paleolithic, specimens of the larger three species, but not of the smaller two foxes, are available.

Choice of Characters for Israeli Guilds

Like earlier researchers, we emphasized that trophic apparati and not general measures of body size should be studied when one seeks ecological character displacement. We studied the trophic apparati directly related to the killing behavior of carnivores: their specialized dentitions. In the Carnivora, the emphasis is on the canine and carnassial teeth (e.g., Gromova 1968; Savage and Long 1986). In the mustelid/viverrid and small-felid carnivore guilds, we focused particularly on the maximal diameter of their upper canines. These carnivores have often been reported to kill their prey by inserting an upper canine between two particular vertebrae in the region where the thoracic and cervical vertebrae meet, then dislocating them, thus lacerating the spinal chord (see, for example, Gossow 1970; Heidt 1972; Leyhausen 1979). We therefore hypothesized that the maximal diameter of the upper canine, used for pushing the vertebrae apart, would be the feature most likely to show size displacement if resource partitioning by different prey size does indeed occur. In these small predators, canines may well reflect the typical size of prey; they would be

adapted to the particular vertebral size and structure most frequently encountered (Leyhausen 1965, 1979).

Canids, by contrast, do not kill their prey by a stylized death bite. They are generally more omnivorous, and they do not possess morphological specializations enabling them to bring down large prey as quickly and efficiently as do cats and mustelids (Kleiman and Eisenberg 1973). Their canine teeth are relatively large but not particularly sharp. They are not specifically adapted to deliver a highly oriented, lethal bite (Ewer 1973); neither are they as strong as the canines of felids (Van Valkenburgh and Ruff 1987). Canids kill their prey through a series of slashing bites (Ewer 1973; Leyhausen 1979), and small prey are killed by violent shaking (Seitz 1950). Because the rostrum of canids is long, the shearing power of the jaws is quite reduced, except near the angle of the jaw itself (Kleiman and Eisenberg 1973). This morphology dictates much less bite strength in the canines as compared with the shearing power of the carnassials. In carnivores with shorter rostra, the difference between bite strength at the carnassials and that at the canines is not as pronounced.

Sexual Size Dimorphism

Two of our Israeli carnivore guilds contained highly dimorphic species. One possible interpretation of the evolution of sexual size dimorphism is that it reduces resource overlap and competition between males and females (reviewed by Hedrick and Temeles 1989; Shine 1989). An extensive literature deals specifically with the marked sexual size dimorphism of mustelids (for review, see King 1989).

Several studies of sexual size dimorphism in weasels concluded that it is adaptive for reducing intersexual food competition. Brown and Lasiewski (1972) argued that elongate mustelids are more dimorphic than less elongate species of equal body mass because elongation increases energy needs and consequently increases intersexual competition for food. Simms (1979) used an estimate of body diameter as an index of size and demonstrated a good match between estimated body diameter (and therefore minimum tunnel width) of weasels and minimum tunnel width of likely available prey. He argued that sexual dimorphism in the three North American weasels is at least partly a consequence of intraspecific resource partitioning. Gliwicz (1988), however, suggested that the sexual size dimorphism stems from the fact that pregnancy substantially changes the female body diameter. Since the maximum diameter of weasels should not exceed that of the burrows of their basic prey, females (when not pregnant) are thinner than males and consequently shorter and much smaller. Powell (1979), Moors (1980), and Powell and Leonard (1983) suggested that smaller size was favored in females because it enabled the female to channel more energy into reproduction because of her own reduced needs. A similar model, based on the different energetic needs of

males and females, predicts different optimal body sizes for the two sexes during the breeding season, thereby providing an energetic explanation for sexual size dimorphism (Sandell 1989).

Erlinge (1979) and Moors (1980) suggested that the larger size of the polygynous male weasels results from intrasexual selection favoring large males over small ones in competition for mates. The smaller size of females was seen as adaptive because it permitted them lower maintenance costs and food requirements, especially important during the reproductive period (Erlinge 1979; Moors 1980). Likewise, Moors (1984), in a study of various mustelid species, concluded that sexual dimorphism in body size is not primarily an adaptation to competition. Holmes (1987) examined sexual dimorphism in a number of tooth characteristics in North American weasels and arrived at a similar conclusion. He suggested that sexual dimorphism is not mainly a means of partitioning resources and that the degree of sexual dimorphism in a population of any species is unaffected by the presence or absence of other weasel species.

The ecological interpretation of sexual size dimorphism as a means for reducing resource overlap between the sexes is similar to the idea of size displacement as a means for reducing interspecific resource overlap. Previous studies of sexually dimorphic carnivores, however, did not try to study both hypotheses, but compared males to males and females to females, or else used means of the mean sizes of the two sexes or midpoints of their ranges. Two of our carnivore guilds—the mustelid/viverrid guild and the small-felid guild—comprise species that are dimorphic, albeit to varying degrees, for body size and skull length (see also Moors 1984) and even more dimorphic for canine diameter. For these guilds we viewed each sex as a separate morphospecies and analyzed all morphospecies at once. We reasoned that, if competition for food is a prime selective pressure, then each sex of each species is competing with its conspecific opposite sex plus both sexes of all other species. Thus character displacement should act between sexes of one species just as it does between each sex of that species and the males and females of other species (Dayan et al. 1989a). Intraspecific competition has not been explored as assiduously as interspecific competition has, but where it has been sought it usually seems to be at least as strong as the latter (see, for example, Connell 1983; Abrams 1987a, b).

Canids are not very dimorphic and are less dimorphic than are most mustelids, viverrids, and felids (Ewer 1973). This difference may be related to the fact that monogamy and paternal care are typical of canids but extremely rare in the other families (Kleiman 1977). Ralls (1977) found that monogamous mammals typically have little sexual size dimorphism, whereas extremely polygynous species tend to be very dimorphic. Moors (1980) reported that highly dimorphic species tend to be strongly carnivorous, whereas those with low dimorphism tend to be omnivorous or to eat relatively small prey. Kleiman and Eisenberg (1973) also suggested that the tendency toward omnivory in canids helps to permit pair-bonding, which Ralls (1977) correlates with low sexual

size dimorphism. Whatever the evolutionary reason for the low sexual size dimorphism in canids, we used mixed populations of males and females.

Morphological Patterns

In the mustelid/viverrid and small-felid guilds of Israel (Figures 7.1 and 7.2, respectively), we found a tendency toward size-ratio equality both inter- and intraspecifically in one trait, maximum canine diameter (Dayan et al. 1989a, 1990). This pattern suggests a coevolutionary morphological response of the different species (and sexes) to one another. The species of each guild exhibit some geographic size variation, and their zone of overlap is quite limited geographically, yet where all coexist, in Israel, there is a regular pattern—community-wide character displacement in canine diameter. Skull length, a general measure of size, exhibited no regular pattern, nor did upper carnassial length (Dayan et al. 1989a, 1990; Dayan and Simberloff, unpublished data).

In the Israeli fossil record we find the common weasel (*Mustela nivalis*) (Dayan and Tchernov 1988), which by limb morphology should be grouped with the mustelids/viverrids. The size of the fossil specimens appears quite similar to that of the Recent Egyptian population, and in canine diameter the Recent Egyptian population fits well with the general trend (Dayan et al. 1989a).

For the three members of the Israeli Middle Paleolithic canid guild for which material was available, we found size-ratio equality for lower first molar (carnassial) length, the only trait available for measurement. For the five-member

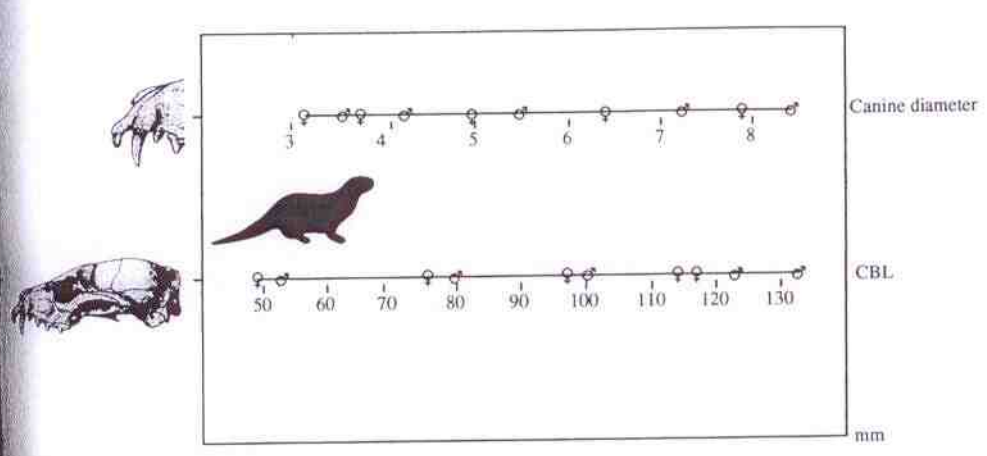

Figure 7.1. Canine diameters and condylobasal skull lengths of species in the mustelid/viverrid guild of Israel.

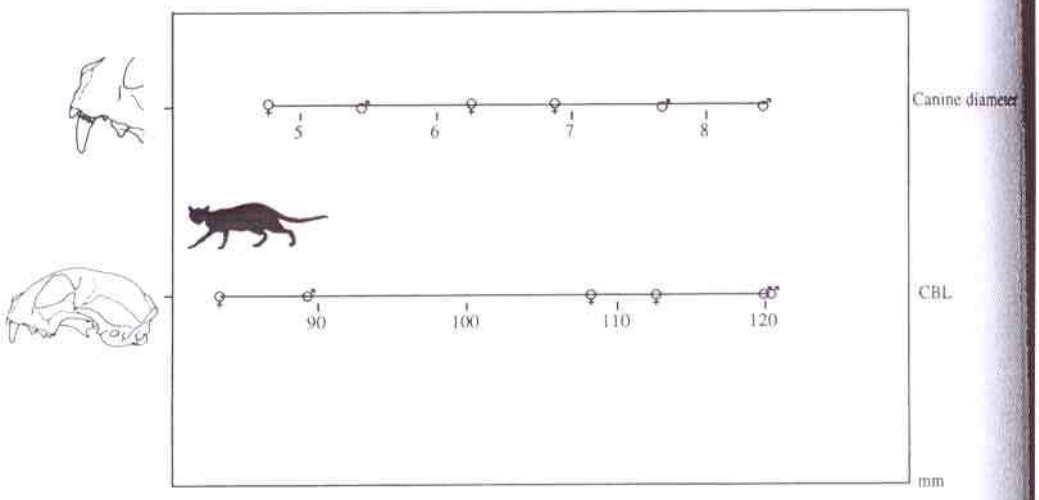

Figure 7.2. Canine diameters and condylobasal skull lengths of species in the small-felid guild of Israel.

Recent guild (Figure 7.3), we found size-ratio equality not only in lower carnassial length but in upper canine diameter and skull length (Dayan et al. 1992a). Thus, the different outcomes for the canids, on the one hand, and the mustelids/viverrids and the felids, on the other, are only partially consistent with our hypotheses. The latter two guilds use their canines in a stylized way, and the canines alone show the predicted regular pattern. The canids do *not* use their canines in this way, and all three traits show a regular pattern. Geographic variation in Israel and North Africa is complex and also not easily interpreted; we discuss these patterns below.

When all three guilds in Israel, or even any pair of them, are viewed together (Figure 7.4), there is no tendency toward size-ratio equality (Simberloff and Dayan 1991). For example, canine diameters of golden jackals, male caracals, and male honey badgers (each in a different guild) are almost identical, as are those of red foxes, male wild cats, and male Egyptian mongooses (also of different guilds). Our hypothesis is that, because of their different locomotor and killing behaviors, the three guilds we posit have characteristically different ways of getting their food and thus qualify as distinct. Unfortunately, there are insufficient dietary data on these species in Israel to determine empirically whether these different behaviors do result in resource partitioning between the designated guilds (Simberloff and Dayan 1991).

Dayan et al. (1989a, b, 1990, 1992a) suggested that ecological character displacement is best manifested by the trophic apparati directly related to feeding ecology, and that other traits, such as body size, are probably more affected by other selective pressures, such as autecological ones. It is quite

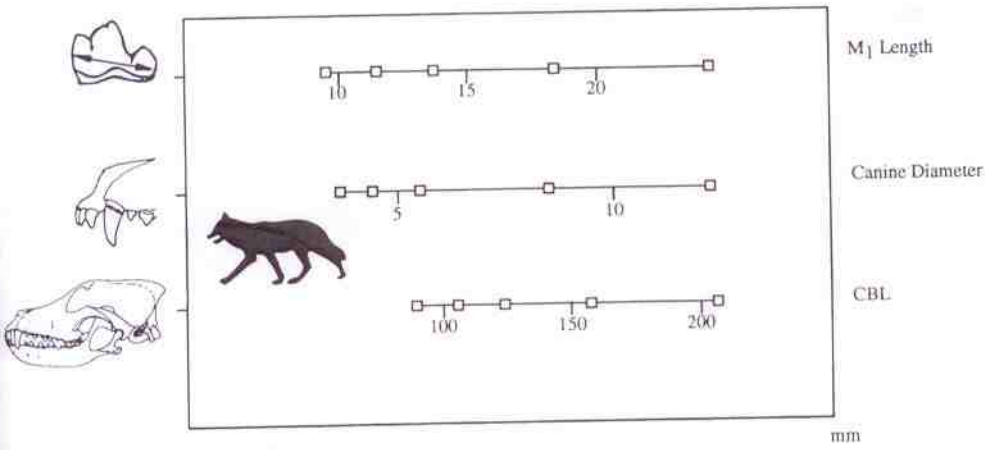

Figure 7.3. Lower carnassial lengths, canine diameters, and condylobasal skull lengths in the canid guild of Israel.

possible that the pattern depicted by body size or skull length is only a passive correlated response to selection acting on the trophic apparati and that choice of unsuitable morphological characters has generated part of the controversy over ecological character displacement and community-wide character displacement. The patterns we found indicate ecological character displacement and community-wide character displacement among Israeli carnivores, but

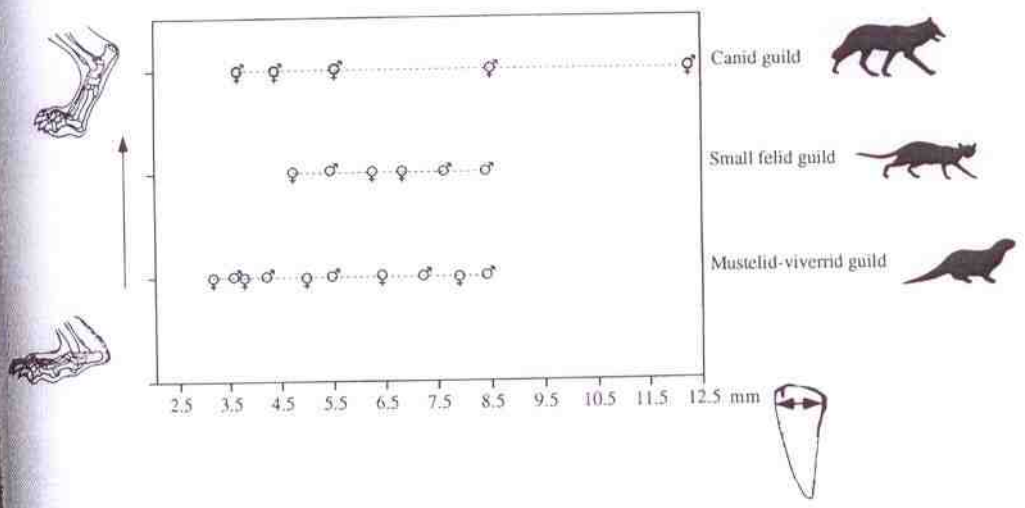

Figure 7.4. Canine diameters of the three carnivore guilds of Israel, as a function of increasing adaptation to cursorial locomotion.

there is currently little direct evidence to verify the ecological interpretation of these phenomena. Because there are very few data in Israel on the food habits of carnivores, we do not know whether niche partitioning through taking different prey-size groups does occur. There has been little research on the functional role of tooth size and skull size in the ability of an individual to bring down prey of different sizes or types (but see Leyhausen 1979). We have only circumstantial evidence that prey are limiting to these species. Clearly, the ecological and evolutionary basis for this phenomenon remains to be studied. The problem of scanty ecological literature on food habits led us to seek other groups of species, elsewhere in the world, for which food habits *have* been reported.

Other Carnivore Guilds and Studies

Several other carnivore guilds in various parts of the world—embracing mustelids, felids, canids, and even hyaenids—have been studied. We, too, examined some New World and Old World mustelids whose food habits have been researched. We studied the three North American weasels that have been the subject of several ecomorphological studies (e.g., NcNab 1971; Ralls and Harvey 1985), and again we found size ratios tending toward equality in upper canine diameters at seven of eight localities studied, but a regular pattern for skull lengths at only four of the eight localities (Dayan et al. 1989a). The ecological literature supports a hypothesis of prey-size selection among the different morphospecies. These weasels, however, are only part of the larger guild of North American mustelids.

We also examined the entire mustelid guild of the British Isles (Dayan and Simberloff 1994). The British mustelids, a subset of mainland European mustelids (from which their populations derive), are the Eurasian badger (*Meles meles*), European pine marten (*Martes martes*), polecat, or European ferret (*Mustela putorius*), stoat (*Mustela erminea*), and least weasel (*Mustela nivalis*). Irish mustelids, whose populations derive from the British populations, form a still smaller subset: the badger, marten, and stoat. Thus the mustelid populations of these two islands form an interesting "natural experiment" (Diamond 1986) for the study of character displacement. In addition to the native mustelid species, in the past few decades farmed American mink (*Mustela vison*) have established feral populations in the British Isles.

Community-wide character displacement was found for canine diameter among mustelids of Great Britain. For skull length it was seen only when the largely vermivorous badger was excluded. When we added feral mink, the regular pattern disappeared, but when we substituted the mink for the polecat, which is now restricted to Wales and adjacent English counties, community-wide character displacement was manifest. For Irish mustelids, size ratios were not equal, but the pattern for canines was more regular than that for skull

lengths. Adding the local feral mink did not result in a regular pattern, but the addition of the mink and exclusion of the badger yielded equal ratios for skull length, though not for canines (Dayan and Simberloff 1994).

A considerable literature is available on the food habits of the European mustelids. The morphological patterns plus the published empirical data on these species support a hypothesis of prey-size partitioning. With the possible exception of the badger, the larger species take somewhat larger prey items, and males take larger prey than do the females, at least during certain times of the year. The significant differences in size between some of the British and Irish populations of the same morphospecies suggest the possibility of ecological release among Irish mustelids, whose populations originally derive from British ones (Dayan and Simberloff 1994). In particular, canine sexual size dimorphism is greater for Irish pine martens, stoats, and mink, as would be expected if there were fewer competitors (Selander 1966). On Ireland, the female pine marten and female stoat are substantially smaller than their counterparts in Great Britain, approaching the sizes of males of missing species (the polecat for the pine marten and the weasel for the stoat). For skull length there is no consistent pattern (Dayan and Simberloff 1994).

We also examined variation in skull length and canine diameter for the native British mustelids and found that five of the six morphospecies occurring on both Ireland and Great Britain had greater coefficients of variation on Ireland (Dayan and Simberloff 1994); most of the differences were significant. This result accords with the "niche-variation" hypothesis (Van Valen 1965; Grant 1967) that morphological variation should increase in the absence of competing species, since competitive release allows different individuals within a population to specialize on different resources. Of course, increased sexual dimorphism could accomplish the same result and is also much greater (for canine diameter) for the pine marten and stoat on Ireland than it is on Great Britain (for the badger, it was lower on Ireland).

Reig (1992) studied morphological variation in the pine marten (*Martes martes*) and the stone marten (*M. foina*) in Europe. Variation in 23 craniodental measurements of pine martens across 15 populations indicated a north-south gradient of increasing skull size. The skulls of stone martens across 13 populations increased in size from west to east. Patterns of variation in sympatric and allopatric samples, and variation in relative size between species within their area of sympatry, suggested no character displacement between species (Reig 1992). Reig studied several characters related to feeding (e.g., length of first lower molar, length of lower canine) but did not measure the upper canines that are used to kill prey. It would be interesting to see whether character displacement between the two species occurs for this trait.

We studied the small felids of the Sind desert of Pakistan, looking at the same characters that we chose for Israeli small felids (Dayan et al. 1990). This guild comprises the same species as does the Israeli guild (wild cat, jungle cat, and caracal) plus another medium-sized cat—the fishing cat (*Felis viverrina*).

For this guild we found a regular pattern of size ratios tending toward equality in canine diameter. The sequence of the morphospecies, however, was different from that of Israel, and this difference reflected an almost twofold difference in sexual size dimorphism between the wild cat of Israel and the wild cat of the Sind desert. For skull lengths and upper carnassial lengths, there was no tendency toward size-ratio equality. This result strongly supports the hypothesis of an ecological role for sexual size dimorphism, at least in the feature used to kill prey (Dayan et al. 1990). The size decreases in the wild cat, jungle cat, and caracal in the Sind, in comparison to their conspecifics in Israel, were also consistent with the hypothesis that the presence of another, slightly larger medium-sized cat in the Sind desert felid guild resulted in ecological character displacement.

North American canids from the Upper Pleistocene were also briefly analyzed. Three large canid species were found in the La Brea tar pits: dire wolves (*Canis dirus*), gray wolves (*C. lupus*), and coyotes (*C. latrans*) (see, for example, Nowak 1979). Size ratios between mean carnassial lengths of these species, determined from data published by Nowak (1979), tend toward equality (Dayan et al. 1993), but new datings of the tar pits are now available (Marcus and Berger 1984), and this research should be carried out thoroughly, without time-averaging of the specimens (Dayan et al. 1993). Such a study is currently under way.

On the other hand, Van Valkenburgh and Wayne (1994), who examined three sympatric jackal species, arrived at conclusions very different from those we have reached in our research. The geographic ranges of the three species—the side-striped jackal (*Canis adustus*), the golden jackal (*C. aureus*), and the black-backed jackal (*C. mesomelas*)—overlap only in East Africa. Van Valkenburgh and Wayne (1994) measured 62 cranial, dental, and mandibular traits, including lengths of upper and lower carnassials and upper canine length. They tested four predicted results of competition: (1) divergence in size should be pronounced in locations where all three species are present, (2) the addition of a third species in East Africa should result in character displacement either in the invading species or in the resident species most similar to it, in characters related to the diet, (3) intraspecific morphological variability should be higher in areas with fewer coexisting species, and (4) species should be less sexually dimorphic when sympatric with more different species. Thus, sexual dimorphism should be least in East Africa. Van Valkenburgh and Wayne (1994) found no evidence for size divergence among these jackals; in fact, the three species appear to converge in size. But they did find character divergence and probable niche compression of black-backed jackals, as evidenced by adaptations for increased carnivory, reduced sexual dimorphism, and reduced variability. The response was asymmetric and affected this species alone (Van Valkenburgh and Wayne 1994).

Werdelin (1993) studied late Miocene and earliest Pliocene hyaenids from several localities in Eurasia and Africa. These hyenas were for the most part

small to medium-sized carnivores with no strong adaptations to the type of bone-cracking scavenging seen in modern-day hyenas. Rather, they have been characterized as "doglike" by Werdelin and Solounias (1991), showing remarkable resemblances to canids in their skull and dental morphology and probably in postcranial morphology as well (Werdelin 1993). Sexual size dimorphism for these species was low. Because of their resemblance to extant canids, Werdelin (1993) explored the possibility that they would show the same pattern of community-wide character displacement in carnassial length that Dayan et al. (1989b, 1992a) found for canids. He found size ratios tending toward equality among the carnassials of sympatric late Miocene hyenas. This pattern was not exhibited by the lower third premolar. This finding indicates the process of community-wide character displacement among these species, operating on their specialized dentitions, although the question of how the pattern arose is even more difficult to resolve for extinct taxa than for extant ones (Werdelin 1993).

Alternative Hypotheses and Unresolved Issues

The results of studies of ecological character displacement in carnivores leave us with several issues that still require careful study. It is also important that we search for alternative hypotheses that might explain the morphological patterns described. For canine diameter, one alternative hypothesis has been suggested, but it is unlikely that it holds.

An Alternative Behavioral Hypothesis

Canines may be used for interspecific communication in threat behavior; in carnivores, at least part of such behavior consists of showing the teeth by opening the mouth and, in some species, by a stylized raising of the lip to bare the canines further (Ewer 1973). Dayan et al. (1989a) tentatively raised the alternative hypothesis that selection entailed aggressive behavior rather than partitioning of prey but found the existing data insufficient to test this idea.

Bekoff (1989), reviewing the literature on the behavioral development of terrestrial carnivores, found few studies of mustelids. Poole (1966) described a "defensive threat," in which a polecat stands with arched back and raised head, facing its aggressor with bared teeth and hissing or screaming. This behavior is carried out generally after, not before, combat, by the individual wanting to *avoid* further aggression, not by the aggressor, who is given wide berth (Poole 1967). Opening the mouth and baring the teeth is a behavior also described, but not discussed, for weasels (Gossow 1970). The discussion by Neal (1986) of badger social behavior mentioned no display of teeth, whereas the extensive description by Kruuk (1989) of the aggressive and defensive

behavior of badgers included a depauperate set of visual cues and no tooth display. Generally, mustelids have well-developed scent glands that are used for marking territories (Gorman and Trowbridge 1989). In fact, Lockie (1966) suggested that the idea of visual display derives largely from avian studies, whereas small carnivores lay scent or use other territorial markers, avoiding face-to-face encounters. This very limited literature may indicate that baring teeth is relatively unimportant in mustelids, except perhaps in defensive behavior, and that it is unlikely that evolution would have calibrated canine size differences among mustelids in response to this selective pressure.

Canid and felid behaviors have received more study. Threat behavior in cats has been carefully described and includes various visual cues, among them a variety of facial expressions (Leyhausen 1979), which are graphically represented by Bradshaw (1992); these include opening the mouth. Kleiman and Eisenberg (1973) suggest that the facial expressions of canids appear more exaggerated than do those of felids. During display, some canids, including the gray wolf (Kleiman 1967) and the golden jackal (Seitz 1959), curl up their lips to bare the canine teeth. The longer muzzle of canids may contribute to the appearance of greater expression in canids than in felids, especially during threat, when the canid muzzle becomes wrinkled and the teeth are bared (Kleiman and Eisenberg 1973).

A basic problem with a hypothesis relating canine size ratios to behavior is that no behavioral models treat interspecific size ratios. Furthermore, the fact that we are dealing with different species and differing social systems would greatly complicate a possible behavioral model (Dayan et al. 1989a). But even were such a model to be erected, we would still have to explain why canids, in which baring the canines is so prominent, exhibit a regular pattern not only in the canine teeth but also in carnassials and skull lengths, whereas mustelids, in which this visual cue appears to be unimportant, nevertheless exhibit canine diameter regularity but do not have the sizes of the carnassials or skulls equally spaced. Finally, it should be noted that, for felids, this pattern occurs for canine diameter and not for canine length (Dayan et al. 1990), which might be of more obvious visual significance. For other groups, canine lengths were not measured. In sum, it appears to us that the most parsimonious explanation for the canine pattern we found so consistently in all of our carnivore studies is that it is generated by selective pressure to partition prey according to prey size.

Remaining Problems

If this explanation is correct, then the fact that all three traits show interspecific size-ratio equality in canids is an important problem for future study. Why should there be size-ratio equality for canine diameter in the canids, which do not use their canines as the felids and mustelids/viverrids do? Related

puzzling observations come from North Africa, where the largest (wolf) and smallest (Blanford's fox) of the five Israeli canid species are missing (Dayan et al. 1992a). The golden jackal subspecies in Egypt, *Canis aureus lupaster,* is very large in canine diameter, lower carnassial length, and skull length. For all three traits it is roughly midway in size between the Israeli populations of wolves and golden jackals. In other words, it appears to have undergone ecological release in the absence of the wolf. The wolf, however, is missing from all of North Africa, yet the golden jackal shows clines of decreasing canine diameter and skull length from east to west, whereas the carnassials remain unchanged (and very large relative to those of the Israeli population). In Algeria, for example, jackal size is identical to that in Israel, as measured for both canines and skulls, whereas the carnassials equal those of the Egyptian population. What selective pressures are at work here?

In contrast, carnassial length does *not* decrease from Israel to Egypt for Ruppell's sand fox, despite the absence of the smaller Blanford's fox, and it appears to stay constant all across North Africa (Dayan et al. 1992a). Of course, one might not have expected diminution, given the resource bases in the different sites, but these are unknown. At the same time, the canine diameter of Ruppell's sand fox *does* seem to decrease in Egypt, as does skull length. Both increase again in Algeria, though not to the sizes in Israel (Dayan et al. 1992a). An ANOVA shows no significance differences in either trait, but sample sizes are very small. It would be interesting to determine whether, with adequate samples, these results hold.

Another unstudied problem is the difference in sexual dimorphism between canids and the other groups. As noted above, the reduced sexual dimorphism in canids may reflect the monogamy and paternal care that typify canids but are rare in the other families. Moreover, the more omnivorous habits of canids, relative to those of felids, mustelids, and viverrids, may also contribute to reduced sexual dimorphism. A study of a wide range of carnivores and a phylogenetic analysis of the wide range of carnivores would help to determine the causes of this pattern (see Gittleman and Van Valkenburgh, in prep.).

Finally, we have not established with field data that the three guilds we posit are actually partitioning resources in Israel, though the hypothesis is reasonable on the basis of their locomotor behavior. The patterns of size-ratio equality obtain within each guild in Israel, but not when the three guilds are combined into one overarching carnivore guild (Simberloff and Dayan 1991). But Van Valkenburgh and Wayne (1994:1577), following Wayne et al. (1989), imply that competition is likely between members of each of the different guilds:

> In our previous study on jackals we hypothesized that a constraint on body size divergence is the unique richness in East Africa of other carnivore taxa, both larger and smaller than a typical jackal (6–10 kg) (Wayne et al. 1989). There are at least 20 species smaller and seven species larger than the jackals in the Serengeti ecosystem (Kingdon

1977) and a similar diversity exists in South Africa (Smithers 1983). Thus any significant increase or decrease in size might bring the jackals into greater competition with other species.

Van Valkenburgh (1985) similarly defined carnivore guilds containing several families. Clearly, more research is needed on likely bases for guild assignment, and this research will have to be field-oriented.

In sum, we hope that our recent papers have contributed to a clarification of morphological coevolution among carnivores and that carnivores will continue to have a major role in questions of ecomorphology. If the questions that still need to be addressed attract further study, the joint efforts of field ecologists, mammalian morphologists, and paleontologists in these areas should pave the way for a fuller understanding of evolution in carnivore communities.

Acknowledgments

We thank B. Van Valkenburgh, R. K. Wayne, and L. Werdelin, for access to unpublished manuscripts, and I. Zohar, for drawing the figures.

References

Abrams, P. A. 1987a. An analysis of competitive interactions between three hermit crab species. *Oecologia (Berlin)* 72:233–247.

Abrams, P. A. 1987b. Resource partitioning and competition for shells between intertidal hermit crabs on the outer coast of Washington. *Oecologia (Berlin)* 72:248–258.

Arita, H. T. 1993. Tests for morphological competitive displacement: A reassessment of parameters. *Ecology* 74:627–630.

Barton, D. E., and David, F. N. 1956. Some notes on ordered intervals. *J. Roy. Stat. Soc. B* 18:79–94.

Bekoff, M. 1989. Behavioral development of terrestrial carnivores. In: J. L. Gittleman, ed. *Carnivore Behavior, Ecology, and Evolution*, pp. 89–124. Ithaca, N.Y.: Cornell Univ. Press.

Bergmann, C. 1847. Über die Verhaltnisse der Warmekonomie der Thiere zu ihrer Grosse. *Göttingen Studien* 3:595–708.

Bradshaw, J. W. S. 1992. *The Behavior of the Domestic Cat*. Wallingford, U.K.: CAB International.

Brown, J. H., and Lasiewski, R. C. 1972. Metabolism of weasels: The costs of being long and thin. *Ecology* 53:939–943.

Brown, W. L., and Wilson, E. O. 1956. Character displacement. *Syst. Zool.* 5:49–64.

Clutton-Brock, J., Corbet, G. B., and Hills, M. 1976. A review of the family Canidae with a classification by numerical methods. *Bull. British Mus. (Nat. Hist.) Zool.* 29(3):1–199.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *Amer. Nat.* 122:661–696.

Davis, S. 1977. Size variation in the fox, *Vulpes vulpes*, in the Palaearctic region today, and in Israel during the Quaternary. *J. Zool. (London)* 182:343–351.

Davis, S. J. M. 1981. The effects of temperature change and domestication on the body size of Late Pleistocene to Holocene mammals of Israel. *Paleobiology* 7:101–114.

Dayan, T., and Simberloff, D. 1994. Character displacement, sexual dimorphism, and morphological variation among British and Irish mustelids. *Ecology* 75:1063–1073.

Dayan, T., Simberloff, D., and Tchernov, E. 1993. Morphological change in Quaternary mammals: A role for species interactions. In: R. A. Martin and A. Barnosky, eds. *Morphological Change in Quaternary Mammals of North America: Integrating Case Studies and Evolutionary Theory,* pp. 71–83. Cambridge: Cambridge Univ. Press.

Dayan, T., Simberloff, D., Tchernov, E., and Yom-Tov, Y. 1989a. Inter- and intraspecific character displacement in mustelids. Ecology 70:1526–1539.

Dayan, T., Simberloff, D., Tchernov, E., and Yom-Tov, Y. 1990. Feline canines: Community-wide character displacement among the small cats of Israel. *Amer. Nat.* 136:39–60.

Dayan, T., Simberloff, D., Tchernov, E., and Yom-Tov, Y. 1991. Calibrating the paleothermometer: Climate, communities, and the evolution of size. *Paleobiology* 17:189–199.

Dayan, T., Simberloff, D., Tchernov, E., and Yom-Tov, Y. 1992a. Canine carnassials: Character displacement in the wolves, jackals, and foxes of Israel. *Biol. J. Linn. Soc.* 45:315–331.

Dayan, T., and Tchernov, E. 1988. On the first occurrence of the common weasel (*Mustela nivalis*) in the fossil record of Israel. *Mammalia* 52:165–168.

Dayan, T., Tchernov, E., Simberloff, D., and Yom-Tov, Y. 1992b. Tooth size: Function and coevolution in carnivore guilds. In: P. Smith and E. Tchernov, eds. *Structure, Function and Evolution of the Teeth,* pp. 215–222. London: Freund.

Dayan, T., Tchernov, E., Yom-Tov, Y., and Simberloff, D. 1989b. Ecological character displacement in Saharo-Arabian *Vulpes:* Outfoxing Bergmann's Rule. *Oikos* 55:263–272.

Diamond, J. M. 1986. Overview: Laboratory experiments, field experiments, and natural experiments. In: J. Diamond and T. J. Case, eds. *Community Ecology,* pp. 3–22. New York: Harper and Row.

Erlinge, S. 1979. Adaptive significance of sexual dimorphism in weasels. *Oikos* 33:233–245.

Ewer, R. G. 1973. *The Carnivores.* Ithaca, N.Y.: Cornell Univ. Press.

Fuentes, E. R., and Jaksic, F. M. 1979. Latitudinal size variation of sympatric foxes: Tests of alternative hypotheses. *Ecology* 60:43–47.

Gittleman, J. L. 1985. Carnivore body size: Ecological and taxonomic correlates. *Oecologia* 67:540–554.

Gittleman, J. L., and Van Valkenburgh, B. In prep.

Gliwicz, J. 1988. Sexual dimorphism in small mustelids: Body diameter limitation. *Oikos* 53:411–414.

Gorman, M. L., and Trowbridge, B. J. 1989. The role of odor in the social lives of carnivores. In: J. L. Gittleman, ed. *Carnivore Behavior, Ecology, and Evolution,* pp. 57–88. Ithaca, N.Y.: Cornell Univ. Press.

Gossow, H. 1970. Vergleichende Verhaltenstudien an Marderartigen I. Über Lautausserungen und zum Beuteverhalten. *Z. Tierpsychol.* 27:405–480.

Grant, P. R. 1967. Bill length variability in birds of the Tres Marias Islands, Mexico. *Canadian J. Zool.* 45:805–815.

Grant, P. R. 1972. Convergent and divergent character displacement. *Biol. J. Linn. Soc.* 4:39–68.

Grant, P. R. 1975. The classical case of character displacement. *Evol. Biol.* 8:237–337.

Gromova, G. I. 1968. *Fundamentals of Palaeontology,* Vol. XIII. Jerusalem: Israel Program for Scientific Translations.

Harrison, D. L. 1968. *The Mammals of Arabia.* London: Ernest Benn.

Hawkins, C. P., and MacMahon, J. A. 1989. Guilds: The multiple meanings of a concept. *Ann. Rev. Entomol.* 34:423–451.
Hedrick, A. V., and Temeles, E. J. 1989. The evolution of sexual dimorphism in animals: Hypotheses and tests. *Trends Ecol. Evol.* 4:136–138.
Heidt, G. A. 1972. Anatomical and behavioral aspects of killing and feeding by the least weasel, *Mustela nivalis* L. *Proc. Arkansas Acad. Sci.* 26:53–54.
Holmes, R. T., and Pitelka, F. A. 1968. Food overlap among coexisting sandpipers on northern Alaska tundra. *Syst. Zool.* 17:305–318.
Holmes, T. 1987. Sexual dimorphism in North American weasels with a phylogeny of Mustelidae. Ph.D. dissert., University of Kansas, Lawrence.
Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *Amer. Nat.* 93:145–159.
Jaksic, F. M., and Delibes, M. 1987. A comparative analysis of food-niche relationships and trophic guild structure in two assemblages of vertebrate predators differing in species richness: Causes, correlations, and consequences. *Oecologia* 71:461–472.
Jaksic, F. M., Greene, H. W., and Yanez, J. L. 1981. The guild structure of a community of predatory vertebrates in central Chile. *Oecologia* 49:21–28.
Jiménez, J. E. 1993. Comparative ecology of *Dusicyon* foxes at the Churchill National Reserve in north central Chile. Master's thesis, University of Florida, Gainesville.
Kiltie, R. A. 1984. Size ratios among sympatric Neotropical cats. *Oecologia* 61:411–416.
Kiltie, R. A. 1988. Interspecific size regularities in tropical felid assemblages. *Oecologia* 76:97–105.
King, C. M. 1989. The advantages and disadvantages of small size to weasels, *Mustela* species. In: J. L. Gittleman, ed. *Carnivore Behavior, Ecology, and Evolution,* pp. 302–334. Ithaca, N.Y.: Cornell Univ. Press.
Kingdon, J. 1977. *East African Mammals,* Vol. 3, Part A (Carnivores). London: Academic Press.
Kleiman, D. G. 1967. Some aspects of social behavior in the Canidae. *Amer. Zool.* 7:365–372.
Kleiman, D. G. 1977. Monogamy in mammals. *Quart. Rev. Biol.* 52:39–69.
Kleiman, D. G., and Eisenberg, J. F. 1973. Comparison of canid and felid social systems from an evolutionary perspective. *Anim. Behav.* 21:637–659.
Klein, R. G. 1986. Carnivore size and Quaternary climatic change in southern Africa. *Quaternary Res.* 26:153–170.
Kruuk, H. 1989. *The Social Badger.* Oxford: Oxford Univ. Press.
Kurtén, B. 1965. The Carnivora of the Palestine caves. *Acta Zool. Fennica* 107:1–74.
Lewin, R. 1983. Santa Rosalia was a goat. *Science* 221:636–639.
Leyhausen, P. 1965. Über die funktion der relativen stimmungshierarchie (Dargestellt am Beispiel der phylogenetischen und ontogenetischen Entwicklung des Beutfangs von Raubtieren). *Z. Tierpsychol.* 22:412–494.
Leyhausen, P. 1979. *Cat Behavior.* New York: Garland STPM Press.
Lockie, J. D. 1966. Territory in small carnivores. *Symp. Zool. Soc. London* 18:143–165.
Marcus, L., and Berger, R. 1984. The significance of radiocarbon dates for Rancho La Brea. In: P. S. Martin and R. G. Klein, eds. *Quaternary Extinctions,* pp. 159–183. Tucson: Univ. Arizona Press.
Mayr, E. 1956. Geographical gradients and climatic adaptation. *Evolution* 10:105–108.
Mayr, E. 1963. *Animal Species and Evolution.* Cambridge: Harvard Univ. Press.
McNab, B. K. 1971. On the ecological significance of Bergmann's rule. *Ecology* 52:845–854.

Moors, P. J. 1980. Sexual dimorphism in the body size of mustelids (Mammalia: Carnivora): The role of food habits and breeding systems. *Oikos* 34:147–158.
Moors, P. J. 1984. Coexistence and interspecific competition in the carnivore genus *Mustela*. *Acta Zool. Fennica* 172:37–40.
Neal, E. 1986. *The Natural History of Badgers*. London: Croom Helm.
Novikov, G. A. 1962. *Carnivorous Mammals of the U.S.S.R.* Jerusalem: Israel Program for Scientific Translations.
Nowak, R. 1979. *North American Quaternary Canis*. Monographs of the Museum of Natural History, Univ. Kansas, No. 6.
Osborn, D. J., and Helmy, I. 1980. The contemporary land mammals of Egypt, including Sinai. *Fieldiana Zool.* (new ser.), No. 5.
Pimm, S. L., and Gittleman, J. L. 1990. Carnivores and ecologists on the road to Damascus. *Trends Ecol. Evol.* 5:70–73.
Poole, T. B. 1966. Aggressive play in polecats. *Symp. Zool. Soc. London* 18:23–44.
Poole, T. B. 1967. Aspects of aggressive behaviour in polecats. *Z. Tierpsychol.* 24:351–369.
Powell, R. A. 1979. Mustelid spacing patterns: Variations on a theme by *Mustela*. *Z. Tierpsychol.* 50:153–165.
Powell, R. A., and Leonard, R. D. 1983. Sexual dimorphism and energy expenditure for reproduction in female fisher *Martes pennanti*. *Oikos* 40:166–174.
Ralls, K. 1977. Sexual dimorphism in mammals: Avian models and unanswered questions. *Amer. Nat.* 111:917–938.
Ralls, K., and Harvey, P. H. 1985. Geographic variation in size and sexual dimorphism of North American weasels. *Biol. J. Linn. Soc.* 25:119–167.
Reig, S. 1992. Geographic variation in pine marten (*Martes martes*) and beech marten (*M. foina*) in Europe. *J. Mamm.* 73:744–769.
Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Monogr.* 37:317–350.
Rosenzweig, M. L. 1968. The strategy of body size in mammalian carnivores. *Amer. Midl. Nat.* 80:299–315.
Roth, V. L. 1981. Constancy of size ratios of sympatric species. *Amer. Nat.* 118:394–404.
Sandell, M. 1989. Ecological energetics, optimal body size and sexual size dimorphism: A model applied to the stoat *Mustela erminea* L. *Funct. Ecol.* 3:315–324.
Savage, R. J. H., and Long, M. R. 1986. *Mammal Evolution*. London: British Museum (Natural History).
Schoener, T. W. 1969. Models of optimal size for solitary predators. *Amer. Nat.* 103:277–313.
Schoener, T. W. 1984. Size differences among sympatric, bird-eating hawks: A worldwide survey. In: D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, eds. *Ecological Communities: Conceptual Issues and the Evidence*, pp. 254–281. Princeton, N.J.: Princeton Univ. Press.
Schoener, T. W. 1986. Overview: Kinds of ecological communities—ecology becomes pluralistic. In: J. Diamond and T. J. Case, eds. *Community Ecology*, pp. 467–479. New York: Harper and Row.
Seitz, A. 1950. Untersuchungen über angerborene Verhaltweisen bei Caniden I und II. *Z. Tierpsychol.* 7:1–46.
Seitz, A. 1959. Beobachtungen an handaufgezogenen Goldschakalen (*Canis aureus algirensis* Wagner 1843). *Z. Tierpsychol.* 16:747–771.
Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113–151.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *Quart. Rev. Biol.* 64:419–461.
Simberloff, D. 1989. Pattern analysis and the detection of interactions in natural communities. In: G. Montalenti, A. Renzoni, and A. Anelli, eds. *Proc. III Congresso Societa Italiana di Ecologia, Siena, October 21–24, 1987,* pp. 19–29. Parma: Edizioni Zara.
Simberloff, D., and Boecklen, W. J. 1981. Santa Rosalia reconsidered: Size ratios and competition. *Evolution* 35:1206–1228.
Simberloff, D., and Dayan, T. 1991. Guilds and the structure of ecological communities. *Ann. Rev. Ecol. Syst.* 22:115–143.
Simms, D. A. 1979. North American weasels: Resource utilization and distribution. *Canadian J. Zool.* 57:504–520.
Smithers, R. H. N. 1983. *The Mammals of the Southern African Subregion.* Pretoria, South Africa: Univ. Pretoria Press.
Strong, D. R., Szyska, L. A., and Simberloff, D. 1979. Tests of community-wide character displacement against null hypotheses. *Evolution* 33:897–913.
Taylor, M. E. 1989. Locomotor adaptations by carnivores. In J. L. Gittleman, ed. *Carnivore Behavior, Ecology, and Evolution,* pp. 382–409. Ithaca, N.Y.: Cornell Univ. Press.
Tchernov, E. 1988. The paleobiogeographical history of the southern Levant. In: Y. Yom-Tov and E. Tchernov, eds. *The Zoogeography of Israel,* pp. 159–250. Dordrecht, Netherlands: W. Junk.
Tonkyn, D. W., and Cole, B. J. 1986. The statistical analysis of size ratios. *Amer. Nat.* 128:66–81.
Van Valen, L. 1965. Morphological variation and the width of the ecological niche. *Amer. Nat.* 99:377–390.
Van Valkenburgh, B. 1984. A morphological analysis of ecological separation within past and present carnivore guilds. Ph.D. dissert., The Johns Hopkins University.
Van Valkenburgh, B. 1985. Locomotor diversity within past and present guilds of large predatory mammals. *Paleobiology* 11:406–428.
Van Valkenburgh, B., and Hertel, F. 1993. Tough times at La Brea: Tooth breakage in large carnivores of the Late Pleistocene. *Science* 261:456–459.
Van Valkenburgh, B., and Ruff, C. B. 1987. Canine tooth strength and killing behaviour in large carnivores. *J. Zool. (London)* 212:379–397.
Van Valkenburgh, B., and Wayne, R. K. 1994. Shape divergence associated with size convergence in sympatric East African jackals. *Ecology* 75:1567–1581.
Wayne, R. K., Van Valkenburgh, B., Kat, P. W., Fuller, T. K., Johnson, W. E., and O'Brien, S. J. 1989. Genetic and morphological divergence among sympatric canids. *J. Hered.* 80:447–454.
Werdelin, L. 1993. Community-wide character displacement in the carnassials of Miocene hyenas. Unpublished manuscript.
Werdelin, L., and Solounias, N. 1991. The Hyaenidae: Taxonomy, systematics and evolution. *Fossils Strata* 30:1–104.
Williamson, M. 1972. *The Analysis of Biological Populations.* London: Edward Arnold.
Wilson, D. S. 1975. The adequacy of body size as a niche difference. *Amer. Nat.* 109:769–784.
Yom-Tov, Y., and Tchernov, E., eds. 1988. *The Zoogeography of Israel.* Dordrecht, Netherlands: W. Junk.

View publication stats